RECRUITMENT FAILURE, LIFE HISTORIES, AND LONG-TERM DECLINE OF CARIBBEAN CORALS

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Abstract. Population decline, local extinction, and recovery are profoundly influenced by variation in demography and life-history traits. In open populations, changes in patterns of recruitment may also have a major influence on the size of local populations, particularly for short-lived organisms. We examine here the demographic processes underlying a slow decline of corals on Jamaican reefs, where coral cover has decreased by fourfold over a 16-yr period. We divided the study into three approximately equal intervals (1977–1982, 1982–1987, and 1987–1993) and constructed size-based transition matrices for each of three abundant species of corals (*Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata*) that differ substantially in life history: *Montastrea* is slower-growing, longer-lived, and has lower rates of recruitment than the other two species. Rates of survival, population growth (λ), and recruitment declined substantially over time for all species and the stable size structures became increasingly dominated by small colonies. Elasticity and life table response analysis showed that changes in the persistence of large colonies had the biggest impact on population growth in all species. Simulations indicated that the levels of larval recruitment required to maintain populations at 1977 levels increased sharply over time, even as the actual recruitment rate declined. Recruitment failure was much more important to *A. agaricites* and *L. cucullata* than to *M. annularis*, which could survive long periods with minimal larval input. Recovery of these populations will require an increase in both survival and recruitment. The likelihood of the latter will depend on the scale of larval dispersal, and on the impact of large-scale mortality of adults on stock-recruitment relationships. Differences in connectivity and life histories of corals will determine future patterns of recovery or further decline.

Key words: Agaricia agaricites; coral reefs; demography; Leptoseris cucullata; life histories; matrix models; Montastrea annularis; population dynamics; recruitment; sensitivity analysis.

INTRODUCTION

The open nature of marine systems poses a unique set of issues for understanding the dynamics of populations and communities. Even undisturbed populations of site-attached adults such as barnacles, corals, and demersal fishes will go extinct within a generation if their offspring are widely dispersed and recruitment from elsewhere fails. Conversely, localized extinctions caused by acute events (such as hurricanes, ice scour, or an oil spill) are often quickly reversed by recruitment of propagules from upstream sources (e.g., Jackson et al. 1989, Aberg 1992, Connell et al. 1997). The degree of connectivity between local populations varies among marine species, depending on patterns of larval dispersal and recruitment. In some species the larval phase is truncated and local populations are largely self seeded. More typically, larvae are widely dispersed among local populations which collectively comprise a metapopulation (e.g., Gaines and Lafferty 1995, Roughgarden et al. 1985, Caley et al. 1996). Recruitment

failure has a greater impact on short-lived species that are composed of one or a few cohorts. In contrast, longer-lived taxa are buffered against fluctuations in recruitment (the storage effect, sensu Warner and Chesson 1985).

Clearly, the effects on marine species of elevated rates of mortality (e.g., due to natural disturbances or overexploitation) also depend on their life histories and patterns of recruitment (e.g., Munro 1983, Hughes 1984, 1990, Aberg 1992, Gaines and Lafferty 1995, Jackson 1997). The best evidence comes from the applied fisheries literature (see review by Jennings and Kaiser 1998): The abundance of short-lived species with early maturation times and high fecundities typically fluctuates greatly, especially in response to variation in recruitment. Such species can generally be harvested at relatively high intensities and are quick to recover from population crashes, so long as pulses of recruitment continue to maintain the stock size (e.g., Adams 1980). In contrast, slow-growing, long-lived species can only be fished at low intensities and take much longer to recover from over-exploitation, even though the storage effect tends to make them less sensitive to fluctuations in recruitment (e.g., Brander 1981, Jennings and Kaiser 1998). Depending on their life histories, different species vary in their response to the

enhancement of mortality caused by fishing. Consequently, multispecies fisheries often cause a predictable change in taxonomic composition (favoring short-lived species) even where there is relatively little targeting of individual species (e.g., Munro 1983, Russ and Alcala 1998). In turn, natural selection due to sustained harvesting of fishes can also result in evolutionary responses in life histories, such as a reduction in the size at maturation and an increase in fecundity early in life (e.g., Reznick 1993).

In this paper, we examine a sustained, long-term population decline in three species of reef-building corals that vary substantially in life histories and rates of recruitment. Our overall goal is to reveal the demographic processes (e.g., recruitment, growth, mortality) which alter population sizes in open marine systems. We first document long-term changes in abundance of corals over a 16-yr period. Secondly, we describe temporal trends in the demography and recruitment of three targeted species to understand why their abundance has declined. Thirdly, we use matrix modeling to examine further the components of population decline (increasing rates of mortality and shrinkage of colonies, combined with decreasing rates of growth and recruitment), and to quantify their relative importance. We begin this last section by quantifying differences among species and changes over time in terms of size-specific transition probabilities. Then we explore the properties of the transition matrices analytically to compare rates of population growth and stable-size distributions, and to examine the relative importance of different transitions (using elasticities and a life table response analysis). Finally, we use the matrices in simulation studies to examine the effects of declining recruitment. The advantage of this modeling approach is that it integrates numerous impacts on different transitions at different stages of the life cycle, providing a population-level response to environmental change (see, e.g., Harvell et al. 1990, Levin and Huggett 1990, Caswell 1996).

NATURAL HISTORY

We studied three abundant Caribbean corals that differ substantially in life history: *Montastrea annularis, Agaricia agaricites,* and *Leptoseris cucullata.* Different morphs of *M. annularis* probably represent separate species (Knowlton et al. 1992, 1997, Weil and Knowlton 1994, Lopez et al. 1999; but see also Dustan 1975, Fitt et al. 1993, Van Veghel and Bak 1993, Szmant et al. 1997). In deep water, where this study was conducted, *M. annularis* occurs only as thick plates (of uncertain taxonomic status; Weil and Knowlton [1994] state that "the identity of deep water (>30 m) specimens requires further study"), while *A. agaricites* and *L. cucullata* form more delicate, foliaceous colonies. The more robust *Montastrea* is slower growing, a better competitor, and longer lived compared to the other two species (e.g., Lang 1973, Bak and Engel 1979, Bak and Luckhurst 1980, Hughes and Jackson 1985), and is the

main frame builder of many Caribbean coral reefs (e.g., Land and Goreau 1970). *Agaricia* and *L. cucullata* are both brooders, releasing well-developed planulae, while *M. annularis* is a broadcast spawner (Van Moorsel 1983, Szmant 1986, Van Veghel 1994, Knowlton et al. 1997). Rates of recruitment by *M. annularis* are typically much lower than the other two species (e.g., Bak and Engel 1979, Rylaarsdam 1983, Rogers et al. 1984, Hughes and Jackson 1985), although the possibility of rare "mast" years cannot be discounted. Like most clonal organisms, these corals exhibit variable rates of growth, frequently shrinking in size and undergoing asexual fission. A size-based matrix model can readily accommodate these demographic features (e.g., Hughes 1984, Gotelli 1991, Lasker 1991).

Our study was conducted in Jamaica, where the abundance of corals has declined markedly during the last two decades. Megafauna (e.g., turtles, dugongs, and crocodiles) were drastically reduced centuries ago (Jackson 1997), and reef fishes were already severely depleted on the most populated parts of the coastline when the first quantitative fisheries surveys were conducted in the 1960s (Munro 1983). Nonetheless, an extensive literature from the 1950s to late 1970s describes an abundant and diverse coral assemblage (e.g., Goreau 1959, Woodley et al. 1981), which has declined only relatively recently. Two major hurricanes, Allen in 1980 and Gilbert in 1988, caused extensive damage to corals, especially in shallow water (<20 m; see, e.g., Woodley et al. 1981). Corallivorous predators survived the hurricanes better than their prey, hindering the recovery of corals (Knowlton et al. 1981, 1990). In 1983, the most abundant invertebrate macroherbivore, the echinoid *Diadema antillarum,* suffered mass mortalities from disease, which in combination with long-term overfishing of herbivorous fishes, prompted unprecedented and highly persistent blooms of benthic macroalgae (e.g., Hughes et al. 1987, Liddell and Ohlhorst 1992; review by Lessios 1988). Episodes of coral bleaching and localized pollution are also likely to have caused damage (review by Goreau 1992). Hughes (1994) documented a gradual shift in Jamaican benthic community structure since the 1970s, from a coral- to an algal-dominated system. For example, between 1977 and 1993 coral cover at 10 m depth declined from a mean of 52% to only 3% at nine sites located along >250 km of coastline (Hughes 1994). Conversely, cover by fleshy macroalgae at these sites increased from a mean of 4% to 92% (see also Knowlton et al. 1990, Liddell and Ohlhorst 1992, Steneck 1993, Hughes and Connell 2000). Similar long-term and large-scale changes have occurred to a lesser extent on coral reefs in other parts of the Caribbean region (e.g., in Florida [Dustan 1977, Porter and Meier 1992]; the Virgin Islands [Carpenter 1990, Steneck 1993]; the Dutch Antilles [de Ruyter van Steveninck and Bak 1986, Bak and Nieuwland 1995]; the Lesser Antilles [Rogers 1985]; and Panama [Schulman and Robertson 1996]).

In the present study, we recorded long-term demographic changes (in recruitment, mortality, and transition rates between different size classes) for three abundant coral species from 1977 to 1993. The study originally spanned a range of sites and depths (see Hughes and Jackson 1985, Hughes et al. 1987). By 1985 (the midpoint of the study period), corals at all but the deepest site had declined by 73–92%, reflecting the large-scale decline in abundances in shallow water along the north Jamaican coast. Consequently, we focus here on the long-term dynamics of corals in deep water (35 m), where hurricane effects were relatively minor (e.g., Woodley et al. 1981, Hughes 1996) and where algal blooms have been less pronounced compared to shallower sites (Hughes et al. 1987, Liddell and Ohlhorst 1992). Deeper reefs potentially provide a spatial refuge for coral species with wide depth distributions (e.g., *L. cucullata,* Goreau and Wells 1967), and could serve as a source of larvae for seeding recovery in shallower water, where coral cover has fallen much more sharply.

METHODS

The abundance of all corals and the population dynamics (rates of recruitment, asexual fission, growth, and mortality) of the three targeted species were quantified by following the fate of large numbers of colonies for 16 yr, from 1977 to 1993. The colonies were located within twelve 1-m² quadrats that were positioned haphazardly at 35 m depth on Pinnacle 1 Reef, near the Discovery Bay Marine Laboratory on the north coast of Jamaica. Each 0.25 m² ($n = 48$) was photographed 14 times (approximately annually), and every colony was traced, numbered, and digitized to obtain its area at each census (see Hughes and Jackson 1985 for further details). Three categories of colonies were distinguished throughout the study: those that were initially present in 1977, new daughter colonies formed by fission of these older colonies, and new larval recruits. Fission occurred when patches of tissue on larger colonies became separated by partial mortality (although the skeleton always remained intact). Recruits were visible once they reached ~1 cm in diameter. The total number of records (the number of colonies summed over each census) for each species was: *Montastrea annularis,* 1217; *Agaricia agaricites,* 1596; and *Leptoseris cucullata,* 860.

Modeling

To examine further the long-term changes in population dynamics of the corals, we constructed and analyzed size-classified matrix population models for each species. The conventional form of a matrix model is

$$\mathbf{x}(t + 1) = \mathbf{A} \cdot \mathbf{x}(t)$$

where **A** is a matrix describing the probabilities of transition between different age or size classes and **x**(t) is a vector describing the number of individuals in each class at time *t*. The population growth rate is given by the dominant eigenvalue (λ) of the matrix. The speed of convergence to a stable size distribution is given by the ratio of the largest to the next largest eigenvalue: the damping ratio (ρ). To obtain the stable age- or stage-distribution the first right eigenvector (**w**) is calculated, and the relative contribution of each stage to population growth (the reproductive value when the matrix has fecundities) is represented by the first left eigenvector (**v**). The proportional effect on population growth of changes in the transition probabilities is known as the elasticity, and is calculated as

$$\frac{\partial \log \lambda}{\partial \log \lambda} = \frac{a_{ij}}{a_{ij}} \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}$$

(DeKroon et al. 1986, Caswell 1989). To model an open system, we omitted fecundities from the matrix, and instead added externally derived recruits to the local population (Sainsbury 1982, Hughes 1984, 1990, Warner and Hughes 1988, Pascual and Caswell 1991). In this case, λ is <1 (unless asexual reproduction occurs and exceeds mortality), describing the decline of a single cohort or the depletion of a population of mixed ages (Hughes 1984, Aberg 1992).

We arbitrarily divided the study period into three roughly equal intervals of five, five, and six years duration respectively (1977–1982, 1982–1987, and 1987–1993), and constructed separate transition matrices for each species in each period. Three time intervals were chosen to reduce the complexity of comparing all 13 census intervals for each species (39 matrices). An alternative approach would have been to construct matrices that encompassed specific events, such as the 1980 and 1988 hurricanes and the algal bloom from 1983–1993. However, these events often overlapped in time, and using matrices with very different census intervals would preclude comparisons of many of the analytical results.

We used three size classes (small, medium, large), which varied among species due to their markedly different size structures: *Agaricia agaricites* and *Leptoseris cucullata* were divided into size classes of 0–10 cm², 10–50 cm², and >50 cm², while *Montastrea annularis* had larger size classes of 0–50 cm², 50–200 cm², and >200 cm². Transition probabilities were calculated as the proportion of colonies changing size class during each of the three census periods. To test for differences in the transition matrices for the three intervals, we performed a log-linear analysis for each species with the factors initial size (state), fate (final size or death), and time. We used the hierarchical model: frequency = (state × fate) + (state × time), i.e., a model which includes all terms except for interactions involving both fate and time, to determine if fate was significantly affected by time. The effect of species was not incorporated into the analysis because it was appropriate to use different size classes for each, and
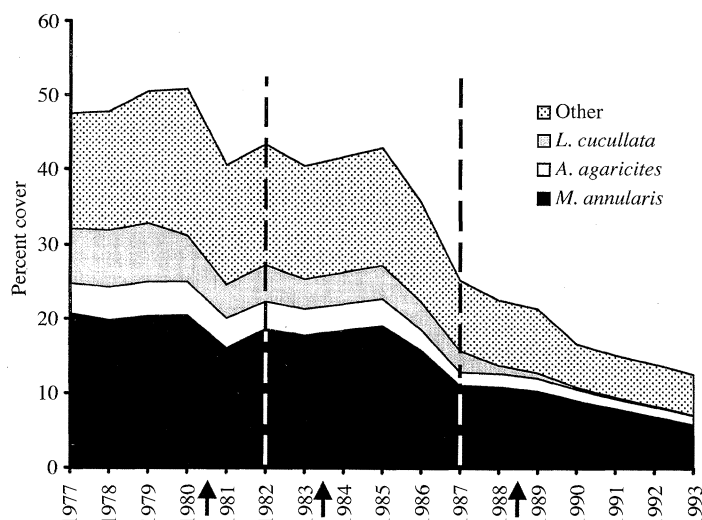
FIG. 1. Percent cover of *Montastrea annularis, Agaricia agaricites, Leptoseris cucullata,* and all other corals in twelve 1-m² plots from 1977 to 1993. The three arrows indicate hurricane Allen (in 1980), the die-off of the echinoid *Diadema antillarum* (in 1983), and hurricane Gilbert (in 1988).

interactions involving species would in part reflect the choice of size classes.

To investigate the population-level consequences of changes in demographic rates, we examined each transition matrix analytically to obtain population growth rates (λ), damping ratios (ρ), eigenvectors (**w, v**) and elasticity matrices (Caswell 1989). To facilitate comparisons of population growth rates and damping ratios, we constructed asymmetrical 95% confidence limits for λ and ρ by bootstrapping. To conduct the bootstrap analyses, individual colonies were randomly selected from the original data, with replacement, until the same number of colonies had been selected as the original sample size. After resampling, a transition matrix was constructed and analyzed, with the entire procedure being repeated for each of 3000 bootstrap iterations. The resulting series of values for each statistic (population growth and damping ratio) was analyzed using the Bias Corrected and Accelerated technique (BC$_a$), to obtain the confidence intervals (Efron and Tibshirani 1993).

The population-level effects of changes in demography over time were examined using a life table response analysis (sensu Caswell 1996). For each species, we calculate the contribution of each matrix element to the change in λ using the initial matrix as a baseline for comparing subsequent matrices (1977–1982 vs. 1982–1987 and 1987–1993). The contributions depend on the magnitude of the change in each matrix element over time, and on the sensitivity of λ to that element. Accordingly, we first calculated a matrix of sensitivities, **S**, using a matrix that was the mean of the initial and one of the subsequent transition matrices. Then, a matrix of contributions was calculated by multiplying each element of **S** by the observed change in each element over the same period (Caswell 1996). This analysis concentrates on the effects on population growth rate of the changes in transition rates,

as opposed to elasticities which show only the potential effects of transitions (regardless of whether or not they changed).

To examine the role of recruitment and to compare the transient population dynamics for each species and time interval, simulations were conducted according to the equation

$$\mathbf{x}(t + 1) = \mathbf{A} \cdot \mathbf{x}(t) + \mathbf{r}$$

where fecundity is omitted from the transition matrix (**A**), and instead a recruitment vector (**r**) is added at each iteration. We began each simulation using the observed population composition for each species in 1977 as the starting vector **x**(0). (This is an arbitrary choice since the population will eventually attain the same stable size distribution regardless of the initial vector.) Using each matrix, we performed two separate simulations: the first examined the depletion of an established population without any recruitment (i.e., **r** = 0), the second included recruitment at the rate observed in the field for that interval. We also calculated the amount of recruitment that would be required to maintain population sizes at the levels observed in 1977. All simulations were carried out for 100 yr (16 or 20 iterations depending on the census interval), by which time equilibrium growth rates had been reached.

RESULTS

Population decline

The percent cover of corals on Pinnacle 1 Reef declined from 47.5% ± 4.1% (mean ± 1 SE) in 1977 to 12.6% ± 2.7% in 1993 (Fig. 1). Cover was steady from 1977–1980, but dropped slightly in 1980–1981, when Hurricane Allen struck Jamaica (Woodley et al. 1981). From 1981 until 1985 coral cover remained just above 40%, but over the next eight years it slowly decreased by a further two-thirds. During this 8-yr period (1985–
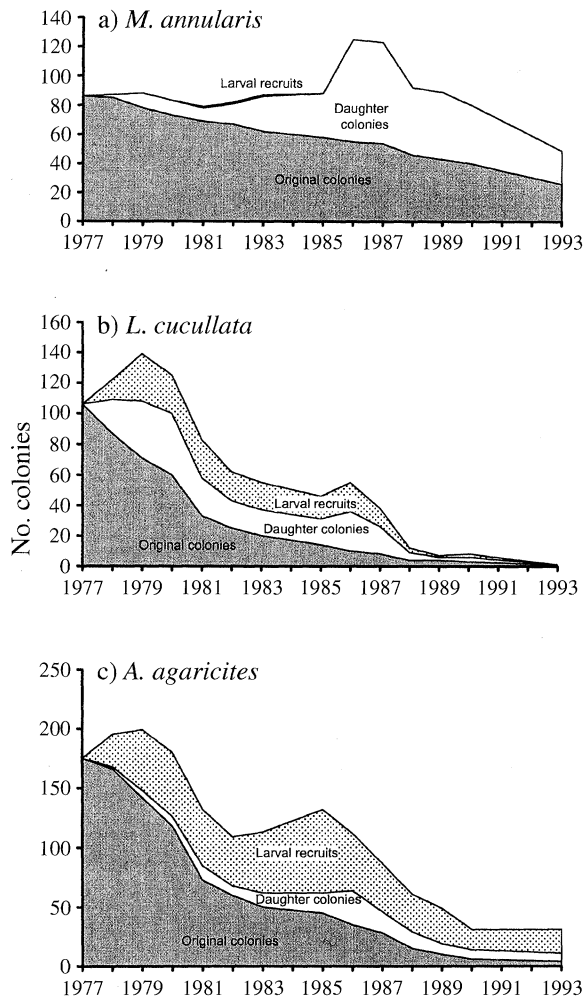
FIG. 2. Number of colonies of *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata* over time. Colonies at each census are divided into three types: those originally present in 1977, daughter colonies formed by fission, and new larval recruits.

1993), cover by fleshy macroalgae on Pinnacle 1 increased from 26% ± 6% to 76% ± 4%, and bare space declined to almost zero (Hughes 1996). The number of coral species within the 12 m² declined, from 17 in 1977 to 11 in 1993. At the outset of the study, *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata* accounted for 67.5% of the total scleractinian cover, occupying 32.1% of the substrate. By 1993, the cover of the three species had declined by almost four-fifths, to 7.1% (Fig. 1), or 56% of the total cover by corals.

The number of colonies also exhibited a long-term decline (Fig. 2). In 1977, *Montastrea annularis* was represented by 86 colonies, *Agaricia agaricites* by 175, and *Leptoseris cucullata* by 106. By 1993, only 40 colonies of *M. annularis*, 17 of *A. agaricites*, and a single colony of *L. cucullata* were present. The first substantial decline in numbers occurred in 1980–1981,

when Hurricane Allen occurred. The number of colonies of the more robust *M. annularis* did not change, but the relatively delicate *A. agaricites* and *L. cucullata* declined in number by 27% and 34%, respectively. Over the next 12 years these latter two species continued to decline, dropping to 18% and 1% of their 1977 abundance by 1993. The number of colonies of *M. annularis* varied little up to 1985, but then increased by 40–42% during 1986 and 1987 (due to fission), before declining steadily up to 1993, to 57% of the original number in 1977 (Fig. 2). Note that the increase in the number of colonies of *M. annularis* in 1986–1987 occurred despite a decline in cover (Figs. 1 and 2).

The three species differed greatly in their rates of mortality and turnover (Fig. 2). Survival of colonies that were already established in 1977 was markedly higher in *Montastrea annularis*; 30% remained alive after 16 yr compared to only 2% of *Agaricia agaricites* and 1% of *Leptoseris cucullata*. As these older colonies declined in number, new colonies were added by asexual fission and larval recruitment. The rate of fission was high for *M. annularis*, intermediate for *L. cucullata*, and low for *A. agaricites* (Fig. 2). Conversely, larval recruitment was by far the lowest for *M. annularis*, and was greatest for *A. agaricites* (Figs. 2 and 3). Until 1985, the majority of colonies of *M. annularis* were the original ones present in 1977. However, a marked increase in the rate of fission of *M. annularis* occurred in 1986–1987, so that from this date onwards, new daughter colonies and older individuals were almost equally abundant. Turnover was higher in the other two species. New colonies outnumbered the original ones from 1983 in *A. agaricites* and from 1981 in *L. cucullata*. For *A. agaricites*, most of the new colonies were larval recruits, while recruits and daughter colonies of *L. cucullata* were approximately equally abundant throughout the study (Fig. 2).

The rate of larval recruitment declined over time (Fig. 3). A total of 294 recruits were recorded at the 14 censuses; 160 in 1977–1982, 101 in 1982–1987, and only 33 in 1987–1993 (Fig. 3). Moreover, only about one-third of these recruits remained alive at the end of each census interval: (55, 35, and 8, respectively). Sixty-nine percent of the recruits were *Agaricia agaricites* and 30% were *Leptoseris cucullata*, while only a single recruit was recorded in 16 years for *Montastrea annularis*, in 1981.

Transition matrices

The population matrices are characterized by high rates of transition between most size classes, reflecting a plastic life cycle which includes variable growth rates, stasis (i.e., staying the same size), fission and colony shrinkage (i.e., transitions from large or medium to small size classes). Transitions were strongly size dependent for all species and times (Table 1). Small colonies invariably had the highest rate of mor-
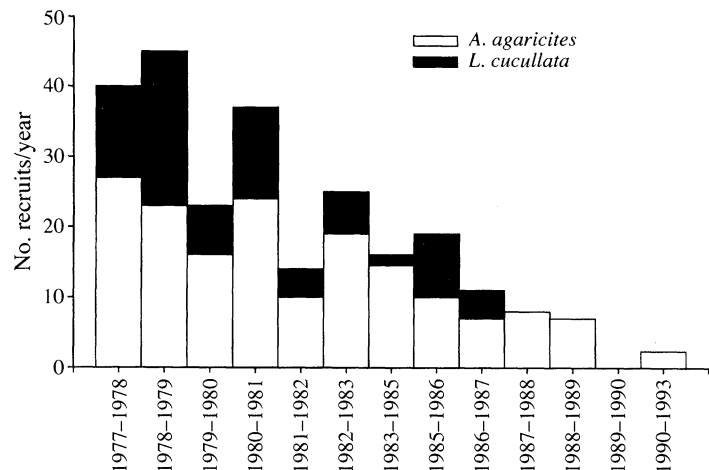
FIG. 3. Rates of recruitment of *Agaricia agaricites* and *Leptoseris cucullata* from 1977 to 1993, into twelve 1-m² plots. *Montastrea annularis* had only one recruit, in 1981.

tality (q_x), and were usually the most likely to increase in size. Larger colonies survived better, but were more likely to shrink or contribute to smaller size classes by fission. Three of the matrices (*Montastrea annularis* in 1977–1982 and 1982–1987, and *Leptoseris cucullata* in 1977–1981) have one or more columns whose transition rates sum to more than one (Table 1), because (from that size class) new colonies generated by fission exceeded losses due to mortality.

The life history differences among species are most clearly observed in the initial matrix (1977–1982), before serious population decline occurred. *Montastrea annularis* had the lowest rate of mortality: only 19%

of the original colonies died in this first 5-yr period, compared to 60% of *Agaricia agaricites* and 77% of *Leptoseris cucullata*. The largest *M. annularis* in particular were virtually immune to mortality in the first (and second) time interval, with only a single colony dying in the first 10 years. In contrast, 27% and 52% of the largest colonies of *A. agaricites* and *L. cucullata*, respectively, died in the first interval (1977–1982, Table 1). These comparisons need to be made cautiously, given the different size categories we used for describing *M. annularis* vs. the other two species. However, even the smallest category of *M. annularis* (colonies <50 cm²) survived better than the largest *L. cucullata*

TABLE 1. Transition matrices, sample sizes, and size-specific mortality rates (q_x) for 1977–1982, 1982–1987, and 1987–1993.

Species and size class	1977–1982 Size class			1982–1987 Size class			1987–1993 Size class		
	I	II	III	I	II	III	I	II	III
Montastrea annularis									
Size class I	0.429	0.227	0.057	0.421	0.583	1	0.049	0.375	0.276
Size class II	0.107	0.5	0.257	0.053	0.583	0.474	0.066	0.188	0.276
Size class III	0	0.091	1.029	0	0.042	0.737	0	0.063	0.241
q_x	0.429	0.136	0.029	0.526	0.125	0	0.885	0.531	0.379
n	28	22	35	19	24	38	61	32	29
Agaricia agaricites									
Size class I	0.034	0.05	0	0	0.102	0.088	0	0.038	0
Size class II	0.125	0.183	0.346	0.217	0.306	0.441	0.111	0.135	0.286
Size class III	0.091	0.233	0.5	0.043	0.102	0.235	0	0.077	0.214
q_x	0.727	0.550	0.269	0.739	0.592	0.412	0.889	0.788	0.571
n	88	60	26	23	49	34	18	52	14
Leptoseris cucullata									
Size class I	0.022	0.053	0.095	0.071	0.05	0.115	0	0	0
Size class II	0.087	0.026	0.381	0.143	0.05	0.308	0	0	0.077
Size class III	0.043	0.158	0.714	0	0.15	0.385	0	0	0
q_x	0.87	0.789	0.524	0.929	0.8	0.654	1	1	0.923
n	46	38	21	14	20	26	7	12	13

Notes: Size classes are 0–50 cm², 50–200 cm², and >200 cm² for *Montastrea annularis*; and 0–10 cm², 10–50 cm², and >50 cm² for *Agaricia 1agaricites* and *Leptoseris cucullata*. The sample size, *n*, is the number of colonies at the beginning of each interval. Transitions from a given size class are in columns. Matrix elements and q_x are proportions.

TABLE 2. Population growth rates (eigenvalues, λ) and damping ratios (ρ) for *Montastrea annularis, Agaricia agaricites,* and *Leptoseris cucullata,* based on transition matrices for 1977–1982, 1982–1987, and 1987–1993 (see Table 1).

Species	Census interval	λ	95% CI	ρ	95% CI
Montastrea annularis	1977–1982	1.074	(0.895, 1.258)	1.84	(1.41, 2.68)
	1982–1987	0.847	(0.660, 1.104)	1.49	(1.04, 2.87)
	1987–1993	0.388	(0.261, 0.529)	2.7	(1.16, 10.16)
Agaricia agaricites	1977–1982	0.673	(0.523, 0.864)	9.77	(5.04, 76.83)
	1982–1987	0.531	(0.400, 0.695)	7.18	(3.41, 87.22)
	1987–1993	0.330	(0.188, 0.519)	5.44	(2.58, ∞)
Leptoseris cucullata	1977–1982	0.801	(0.410, 1.722)	10.83	(2.26, 41.19)
	1982–1987	0.503	(0.252, 1.080)	7.47	(2.16, ∞)

(>50 cm²; 43% vs. 52% mortality, respectively, see Table 1). As noted above, recruitment rates and population structures also varied substantially between the three species.

A colony's fate was affected by time (i.e., transition probabilities varied significantly among the census intervals) for all three species (log-linear analyses; *Montastrea annularis,* $\chi^2_{18} = 116$, $P \ll 0.001$; *Agaricia agaricites,* $\chi^2_{18} = 31.6$, $P = 0.025$; *Leptoseris cucullata,* $\chi^2_{18} = 29.5$, $P = 0.042$), consequently, the matrices for each period were distinctive. In general, rates of mortality and shrinkage increased over time (especially in the third period), while rates of colony growth and stasis declined (Table 1). For *M. annularis,* overall mortality rates were 19%, 16%, and 67% respectively for the three periods. Size-specific mortality rates increased consistently over time across all size-classes, especially for the largest colonies (size class III), where 3%, 0%, and 38% died in the three intervals. Similarly, overall rates of mortality of *A. agaricites* were 60%, 57%, and 77% for the three periods, with the biggest increase occurring in large colonies (27%, 41%, and 57% mortality, respectively). Overall mortality rates for *L. cucullata* were 77% for both 1977–1982 and 1982–1987, rising to almost 100% in the final period (of 32 colonies alive in 1987, only one survived to 1993), which obviously precluded construction of a useful matrix for that period. Note that overall rates of mortality in the first and second intervals were essentially the same for all three species, even though size-specific rates consistently increased (Table 1). This disparity occurred because there were proportionally fewer small colonies (with high mortality rates) in 1982–1987 than in the previous interval (see Table 1 for sample sizes), which boosted overall survival despite worsening rates of attrition in each size-class.

Another important change occurred in rates of stasis or retention of colonies (the probability of staying the same size), particularly in the largest size class (Table 1). This "transition" (the bottom-right element of the matrices) steadily declined over time in all species, due to the increased rate of mortality and shrinkage of the largest colonies. In *Montastrea annularis,* this transition fell over time from 1.03 to 0.74, and finally to only 0.24. Similarly, retention rates for the largest

Agaricia agaricites dropped from 0.50 to 0.23 and then 0.21, while those for *Leptoseris cucullata* declined from 0.71 in 1977–1982 to 0.38 in 1982–1987. In the third interval, 12 out of the remaining 13 large colonies of *L. cucullata* died and the sole survivor shrank, giving a retention rate of zero.

Analysis of matrix properties

The dominant eigenvalues (λ) for all three species declined sharply over time (Table 2), indicating that the rate of depletion of each population was accelerating. In the initial period, survival of *Montastrea annularis* was substantially higher than the other species, as would be expected from previous studies of their life histories (e.g., Bak and Luckhurst 1980, Hughes and Jackson 1985). Indeed, λ for *M. annularis* in 1977–1982 was 1.07 (equivalent to an annual population growth rate of 1.4% per year), indicating that populations in that period were capable of growing slowly by asexual fission even with little or no larval recruitment. In 1982–1987, λ for this species dropped to 0.85 (although the 95% confidence limits still include values slightly greater than one; Table 1). At this rate of depletion, the population would decline by 50% every 20 yr, assuming no further larval recruitment. By 1987–1993, *Montastrea* was declining very rapidly, at a similar rate to the other species, with a population growth rate of only 0.39 (i.e., a decline of more than 95% every 20 yr). Ninety-five percent confidence intervals indicated that survival of *M. annularis* was significantly less in the final interval than either of the first two, while survival of *Agaricia agaricites* was also significantly lower in the final interval; *Montastrea* survived significantly better than *A. agaricites* only in the first interval. The decline in survival of *Leptoseris cucullata* is less clear cut because of the larger confidence limits, but the downward trend over time is the same (Table 2). Lambda for this species in 1987–1993 was almost zero since only a single colony survived the final period (Fig. 2).

The damping ratio, ρ, measures the rate of convergence of a cohort to a stable size structure (regardless of whether a population is increasing or decreasing). The ratio showed a declining trend over time for *Agaricia agaricites* and *Leptoseris cucullata* (Table 2). This
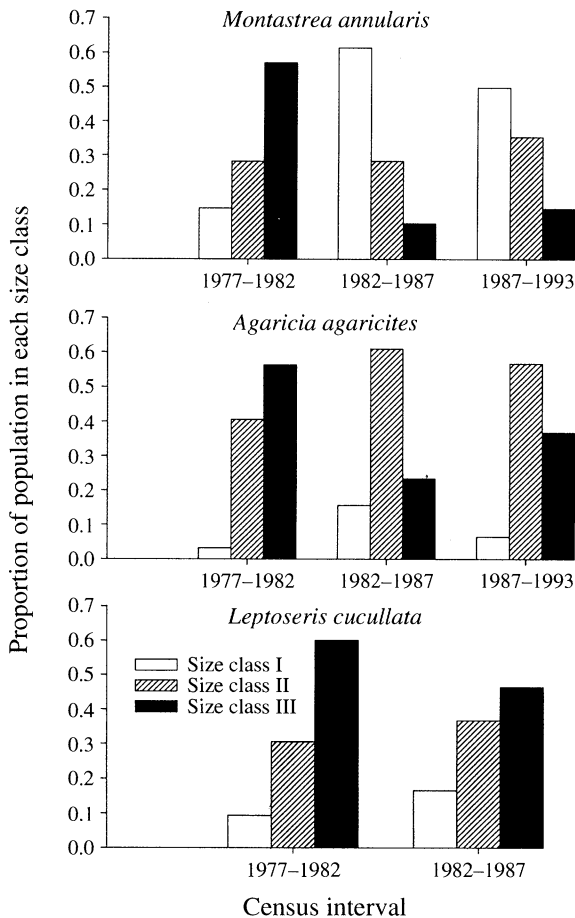
FIG. 4. The stable population structures of *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata* based on transition matrices for 1977–1982, 1982–1987, and 1987–1993 (see Table 1).

is the expected result due to increasing rates of mortality and shrinkage (Table 1), which would make it more difficult for small colonies to attain a large size. The damping ratio for *M. annularis* is substantially lower than for the other species, and shows little change over time, indicating consistently slower rates of growth and mortality than *A. agaricites* and *L. cucullata,* and a much slower convergence to a stable size structure. The asymmetric confidence limits around ρ are very large in most cases (except for *M. annularis* in the first two intervals), and their upper value in particular increases over time (Table 2). This points to the importance of large colonies; bootstrap iterations which by chance included a smaller proportion of large colonies resulted in substantially higher damping ratios, i.e., faster times to attain an equilibrium population structure.

The stable size distribution calculated for each of the matrices became increasingly dominated by small colonies over time (Fig. 4), indicating that a cohort of recruits exposed to conditions early on in the study would eventually achieve a larger mean size than recruits which settled later on. For the initial matrices (1977–1981), the stable composition of each species was dominated by large- and medium-sized colonies, with only 5–15% occurring in the smallest size class, depending on species. For the later matrices (1982–1987 and 1987–1993), the predominance of larger colonies at equilibrium declined, especially in *Montastrea annularis,* where the proportion of colonies in the largest size class dwindled by fourfold, from 57% for the initial matrix to 12% and 15%, respectively.

Elasticities, a measure of the relative contribution of each individual transition to λ varied substantially over time (Table 3). The retention rate of large colonies was almost always the single-most important transition, especially for the first period and for *Montastrea annularis.* Later on, stasis and growth of medium-sized colonies also contributed significantly to λ (i.e., these elements

TABLE 3. Elasticity matrices for *Montastrea annularis, Agaricia agaricites,* and *Leptoseris cucullata*; showing the proportional sensitivity of λ to changes in each element of the transition matrices (see Table 1).

Species	Size class, 1977–1982			Size class, 1982–1987			Size class, 1987–1993		
	I	II	III	I	II	III	I	II	III
Montastrea annularis									
Size class I	0.002	0.003	0.001	0.041	0.025	0.016	0.016	0.082	0.026
Size class II	0.004	0.036	0.037	0.042	**0.200**	0.063	**0.110**	**0.210**	**0.130**
Size class III	0	0.038	**0.880**	0	0.079	**0.530**	0	**0.160**	**0.260**
Agaricia agaricites									
Size class I	0	0.009	0	0	0.059	0.020	0	0.015	0
Size class II	0.004	0.071	**0.190**	0.059	**0.330**	**0.180**	0.015	**0.150**	**0.210**
Size class III	0.006	**0.180**	**0.540**	0.020	**0.180**	**0.160**	0	**0.210**	**0.390**
Leptoseris cucullata									
Size class I	0	0.002	0.008	0.004	0.007	0.020			
Size class II	0.003	0.003	0.089	0.027	0.021	**0.160**			
Size class III	0.007	0.090	**0.800**	0	**0.180**	**0.580**			

Note: Elements >0.1 are indicated in bold.

TABLE 4. Contribution of each transition to the observed declines in population growth rates.

Species and size class	Size class, interval 1–2			Size class, interval 1–3		
	I	II	III	I	II	III
Montastrea annularis						
Size class I	−0.0003	0.0093	0.0200	−0.0131	0.0050	0.0078
Size class II	−0.0149	0.0146	0.0311	0.0078	−0.0580	0.0036
Size class III	0	−0.0473	**−0.2287**	0	−0.0213	**−0.6140**
Agaricia agaricites						
Size class I	−0.0013	0.0103	0.0140	−0.0004	0.0015	−0.0065
Size class II	0.0069	0.0476	0.0295	−0.0004	−0.0148	−0.0196
Size class III	−0.0066	−0.0940	**−0.1518**	0.0053	**−0.1004**	**−0.1956**
Leptoseris cucullata						
Size class I	0.0008	−0.0001	0.0015			
Size class II	0.0028	0.0032	−0.0162			
Size class III	−0.0084	−0.0041	**−0.2801**			

Notes: Positive values indicate that the changes in transitions (between the first and second interval, or between the first and third interval) had a positive effect on population growth. Negative values result from changes in transitions that lead to population decline. Contributions >0.1 are indicated in bold. Matrix elements are proportions.

of the matrix played a proportionately greater role in slowing down the rate of attrition). Transitions to and from the smallest size class had little effect on λ for all species throughout the study. Similarly, a life table response analysis indicates that the reduction in λ over time is overwhelmingly due to the loss of large colonies

FIG. 5. Population size over time for *Montastrea annularis, Agaricia agaricites,* and *Leptoseris cucullata,* based on transition matrices for 1977–1982, 1982–1987, and 1987–1993 (see Table 1), with no recruitment.

(Table 4). Positive values in Table 4 indicate changes in transitions that enhanced population growth, while negative values depict changes that contributed to population decline. The sum of entries in each matrix corresponds approximately to the differences in λs between the initial (1997–1982) and subsequent matrices, which of course are negative (see Table 2). Consequently, most of the changes in transitions recorded during the course of the study had a negative effect on λ.

Simulation studies: recruitment failure

Here we explore the transient behavior of the populations in a series of simulation studies, to examine the role of declining rates of recruitment. We first examine the dynamics of the three species without larval recruitment to project changes in the number of established colonies in populations behaving according to the transitions recorded in each of the three intervals (Table 1). For convenience, we use the population structures of 1977 as a starting point. Our objective is to project the long-term behavior of the populations assuming they continued to act according to the "rules" we measured in each of the three intervals. Since the matrices changed over time, the long-term projections reveal further the consequences of the altered demography of the three species.

The rate of depletion of each species (Fig. 5) was slowest for the initial matrix, intermediate for the middle period, and fastest for the final matrix (as expected from their dominant eigenvalues, Table 2), reflecting the accelerating rate of decline during the 16-yr study. The differences between the three matrices are most dramatic for *Montastrea annularis,* where populations behaving according to the initial matrix grew slowly (at a rate of 7% every 5 yr) due to fission, then slowly declined according to the 1982–1987 matrix (decreasing by 13% every 5 yr), and finally under the third matrix declined rapidly by more than 50% every 5 yr
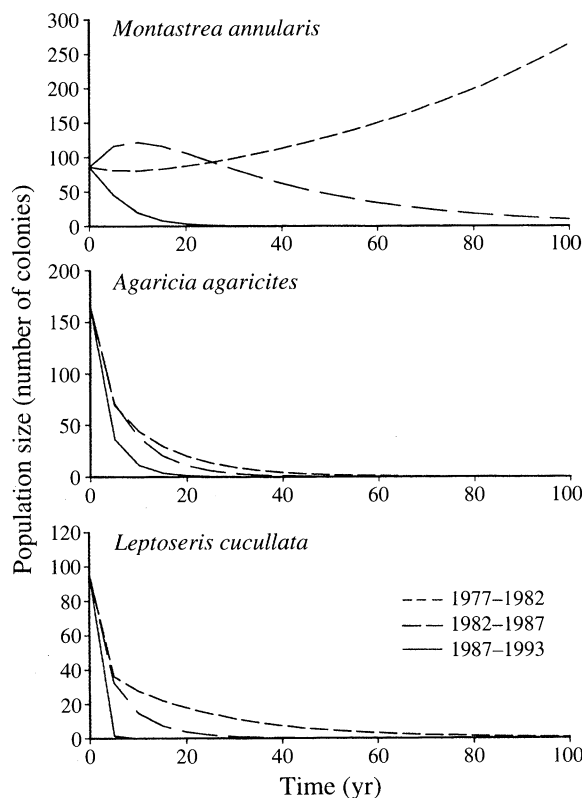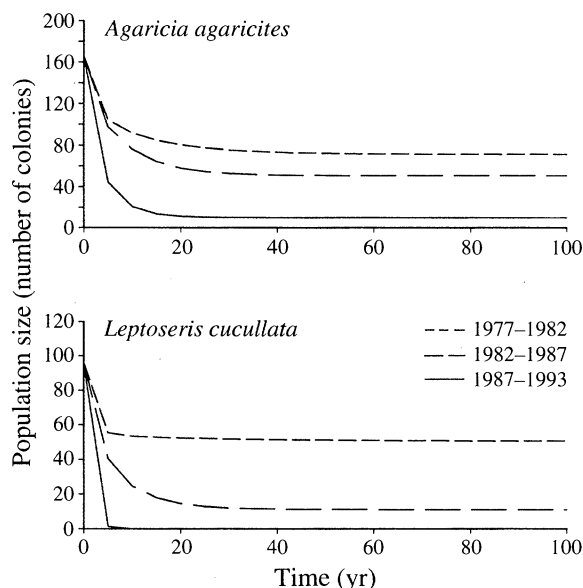
FIG. 6. Population size over time for *Agaricia agaricites* and *Leptoseris cucullata,* based on transition matrices for 1977–1982, 1982–1987, and 1987–1993 (see Table 1), with the observed level of recruitment for each interval. (Recruitment of *Montastrea annularis* was so low that it has no noticeable effect on population size.)

(Fig. 5). Note that these longer-term projections were not initially obvious for two of the matrices: for the 1977–1982 projection, the population first declined, but 20 yr later regained and then began to exceed 1977 levels. Similarly, the 1982–1987 projection grew initially, before declining slowly below initial levels 26 yr later. The rate of depletion of *Agaricia agaricites* and *Leptoseris cucullata* was much more rapid: if conditions recorded during the final 1987–1993 period are projected over time, their populations decline to zero without further recruitment within 10–20 yr (Fig. 5).

The addition of recruitment at each iteration of the simulation will obviously prevent the complete depletion of a population. However, as noted earlier, the observed rate of recruitment declined over time (Fig. 3). Accordingly, we added the observed amount of re-

cruitment during each interval (1977–1982, 1982–1987, and 1987–1993) to each iteration of the matrix projections, to examine the effects of recruitment on long-term changes in population size (Fig. 6). *Montastrea annularis* had only a single recruit in 16 yr, so the addition of recruits to its population was clearly not sufficient to halt the observed declines. For *Agaricia agaricites,* the net rate of recruitment (the number arriving during, and still alive at the end of each of the three time intervals) was 35, 27, and 8, while net recruitment for *Leptoseris cucullata* was 19, 8, and 0 (for the 1977–1982, 1982–1987, and 1987–1993 periods, respectively, Table 5). When these recruits were added to the simulations, the same declining trend occurs over time, indicating the extent to which declining recruitment gains were outstripped by accelerating losses from mortality. For example, for the 1987–1993 matrix, the number of *A. agaricites* equilibrated at only 7% of 1977 levels (and most of the population consisted of the latest cohort of recruits).

We also calculated the amount of recruitment that would be required to maintain population sizes at 1977 levels, for each matrix. As expected, the increasing rates of mortality over time required more and more recruitment to compensate for losses (Table 5). For the 1977–1982 matrices, the number of recruits required every 5 yr to maintain each population was the equivalent of 67% of the original number of colonies (i.e., those present in 1977) for *Agaricia agaricites,* and 47% for *Leptoseris cucullata,* with no recruitment being needed to maintain the population size of *Montastrea annularis.* In contrast, for the 1987–1993 matrices, the proportion of recruits (relative to the number of colonies in 1977) needed to maintain the populations of the three species was 86, 99, and 91%, respectively. However, the observed level of recruitment during this final period was less than one-sixth of that in 1977–1982, and well over an order of magnitude lower than the amount required to maintain rapidly declining populations (Table 5).

DISCUSSION

Life histories and mechanisms of population decline

Our study documents how life history variation among the three species of corals underlies their dif-

TABLE 5. Observed recruitment for each census interval, and the amount that would be required to maintain population sizes at 1977 levels.

Species	Time interval	Observed recruitment	Recruitment needed to maintain population size
Montastrea annularis	1977–1983	1	0
	1983–1987	0	35
	1987–1993	0	73
Agaricia agaricites	1977–1983	35	91
	1983–1987	27	101
	1987–1993	8	144
Leptoseris cucullata	1977–1983	19	49
	1983–1987	8	73
	1987–1993	0	96

ferential susceptibility to elevated rates of mortality and declining recruitment. *Montastrea annularis* was affected most by changes in survivorship, whereas recruitment failure also contributed substantially to the decline of *Agaricia agaricites* and *Leptoseris cucullata*. *Montastrea* had a much higher λ value than the other two species (Table 2) because colonies survived longer and underwent fission more often (Table 1; see also Bak and Engel 1979, Bak and Luckhurst 1980, Hughes and Jackson 1985). Conversely, the damping ratio, ρ, was lower for *M. annularis,* because its colonies are slow growing and take far longer than the other two species to attain a large size (e.g., Hughes and Jackson 1985). Population growth declined sharply over time for all species, indicating that the rate of depletion of each population was accelerating. Similarly, the damping ratios decreased over time for *Agaricia agaricites* and *Leptoseris cucullata* (Table 2), because slower growth rates and higher rates of shrinkage impeded the progression of small colonies into larger size classes, a further indication of populations under stress.

By the end of the study, there were fewer large colonies of all species because many of them had died or had undergone fission, and they had not been replaced by growth of smaller colonies. It is clear that asexual fission of large colonies was not adaptive, especially later on in this study (see also Highsmith 1982, Lasker 1991, McFadden 1991, Smith and Hughes 1999). Fission in these coral species occurs only when colonies are injured (e.g., by partial overgrowth by macroalgae), so that surviving patches of tissue on the same skeleton become separated. Therefore, there is a substantial loss of live cover associated with fission. In addition, small colonies have a much higher rate of mortality than intact, larger ones (Table 1). The large increase in the number of *M. annularis* in 1986–1987 (Fig. 2a) was a symptom of population decline, not growth: coral cover decreased as large colonies were being dismembered into small remnants, many of which were subsequently overgrown and killed by algae.

The accelerating rate of depletion of larger, older colonies is a clear sign of serious population decline, which will take decades or longer to reverse. In particular, a retention rate of only 0.24 for the largest colonies of *Montastrea annularis* in 1987–1993 has major consequences for the persistence of this population, given the length of time necessary to establish these old colonies. At 35 m depth, colonies of this species extend in diameter by a mean of less than 1 cm per year (Hughes and Jackson 1985), i.e., a colony with a diameter of 1 m is at least a century old. Yet in the last 6 yr of this study, nearly 40% of the largest colonies of this species died, while almost all of the survivors were injured, with two-thirds of them shrinking into smaller, more vulnerable size classes (Table 1). These losses are clearly not sustainable, even if rates of recruitment were to increase dramatically. By 1987–1993, the rate of mortality of *M. annularis* was so high

that the population would virtually need to be replaced by new recruits every 6 yr in order to maintain population size at 1977 levels (Table 5). Even then, these colonies would be so small that cover would only be a tiny fraction of that in 1977. Ironically, although *Montastrea* survived the best, its slow rate of recruitment and growth will ensure that it recovers much more slowly than the other species, even if conditions do improve.

Recovery in open systems

Rates of larval recruitment declined sharply over time (Fig. 3), providing only a very small fraction of the number of new colonies needed to maintain population sizes (Fig. 6). Clearly, more recruits and an improvement in survival will be required to ensure recovery. The causes of the decline in recruitment are uncertain. Pre-emption of space by macroalgae is liable to have inhibited settlement, while smothering or overgrowth by algae is likely to have killed new recruits (e.g., Bak and Engel 1979, de Ruyter van Steveninck and Bak 1986, Hughes et al. 1987). Given the large scale of the decline in coral stocks around Jamaica (e.g., Liddell and Ohlhorst 1992, Hughes 1994), it is also possible that the size of the larval pool has decreased. The distinction between these mechanisms of recruitment failure is important. For example, if the decline in recruitment is caused primarily by smothering, a reversal of the algal blooms (e.g., through increased rates of herbivory) would be followed quickly by a pulse of new coral recruits. Conversely, if the breeding stock has declined significantly, there would be a period of much slower colonization by coral recruits, even if free space became widely available. We cannot assume that there is an inexhaustible supply of larval recruits if diminished stock sizes or lower fecundities have altered large-scale stock–recruitment relationships (Lipcius and Van Engel 1990, Peterson and Summerson 1992, Hughes et al. 2000).

The scale of planktonic dispersal of coral propagules in the Caribbean is poorly known, so it is uncertain where the larvae necessary for recovery would come from, if they are not generated locally. Roberts (1997) recently predicted levels of connectivity among Caribbean islands based on large-scale current patterns, assuming that larvae are passively dispersed for 30–60 d. However, coral larvae are capable of settling much sooner; under laboratory conditions peak settlement typically occurs within 2–3 d of release for brooders and 5–10 d for spawners (although a small proportion of a cohort may settle much later, particularly if they are deprived of a suitable substratum; see review by Harrison and Wallace 1990, Wilson and Harrison 1998). Moreover, large-scale variation in recruitment by corals may depend on the size of the upstream breeding stock as well as the distance between sources and sinks. For example, Hughes et al. (2000) showed that regional-scale variation in the fecundity of adult corals

along the Great Barrier Reef explained 72% of the variation in subsequent recruitment by spawning corals. Furthermore, recruitment rates by spawning and brooding corals on the Great Barrier Reef are poorly correlated at all spatial scales, i.e., patterns of water flow do not ensure that locations consistently receive large or small numbers of recruits of all species (Hughes et al. 1999). For brooding corals like *Agaricia agaricites* and *Leptoseris cucullata,* recruitment rates on Jamaican reefs may remain depressed until local breeding stocks recover. Colonization by corals that are capable of long-distance dispersal (e.g., from Cuba) may be less affected, with potentially far-reaching consequences for community structure. Unfortunately, long-lived and slow-growing corals like *M. annularis* will take a century or more to recover to pre-1980 levels even if recruitment resumes quickly.

Long-term population trajectories

Our study demonstrates an accelerating decline of the three coral populations we investigated. In the initial period, the population of *M. annularis* had a stable size distribution, and a very low rate of mortality coupled with a modest rate of asexual fission. Consequently, the population was self sustaining, capable of growing slowly even with negligible levels of larval recruitment (Fig. 5). Hurricane Allen in 1980/1981 caused a slight decline in cover of *M. annularis* (Fig. 1), but it did not affect numbers because most of the tissue loss was through injuries to large colonies. Even including this hurricane, the long-term projection of vital rates during 1977 to 1982 reveals a population that is remarkably resilient. The cover and number of *Agaricia agaricites* and *Leptoseris cucullata* also increased initially, but then dropped in 1980/1981, due to Hurricane Allen, the worst storm for 30 yr (Woodley et al. 1981). Even with Hurricane Allen, population growth rates for 1977–1982 were relatively high: 0.67 for *A. agaricites* and 0.80 for *L. cucullata* (see Table 2 for confidence limits. On an annual basis, λ was 0.92 and 0.96, respectively). At this rate of depletion, for example, 20% of the original colonies of *L. cucullata* would remain alive after 32 yr (in 2009). This relatively slow rate of attrition would normally be balanced by high rates of larval recruitment (as it was in the 3 yr preceding Hurricane Allen, Hughes and Jackson 1985). However, the subsequent changes in demographic rates resulted in this level of depletion (20%) being reached much sooner, after only 6 yr (in 1983; Fig. 2c).

Coral reefs in many parts of the world are being increasingly affected by humans (e.g., reviews by Rogers 1985, Ginsburg 1993, Jackson 1997, Hughes and Connell 2000), and there is an obvious need to understand the degree of change and (more importantly) the underlying mechanisms causing change. The most commonly used attribute for describing the status of a reef is the abundance of corals, usually in terms of total cover: cover going down is "bad", going up is "good".

We caution, however, that coral abundance can easily increase for considerable periods, even in a population which is ultimately destined to decline (and vice-versa). For example, the simulations we conducted use the same matrices iteratively (i.e., rates of mortality and growth are constant), yet they show two examples of reversals in the long-term trajectories of the coral populations (Fig. 6). For the 1977–1982 matrix describing *Montastrea annularis,* the number of colonies first decreased slightly (even though λ was greater than 1), but then increased to exceed the initial levels after 20 yr. Conversely, the 1982–1987 matrix for *M. annularis* describes a population which first grew by over 40% (even though λ was only 0.85), before dropping below starting levels after 26 yr. These reversals arose because the initial population structures differed from the stable distributions of the respective matrices. For example, if a population contained a lower proportion of small, vulnerable colonies than the stable distribution, it could initially grow but then decline even where there is no change in demography. A nonequilibrium size- or age-structure is commonplace in fluctuating environments, and is most likely to occur in species with open populations that receive varying amounts of larval recruitment (such as *Agaricia agaricites* and *Leptoseris cucullata*). Detecting and understanding long-term patterns on coral reefs and elsewhere will be a major challenge, and will require a much longer time frame to investigate than that of most ecological studies.

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